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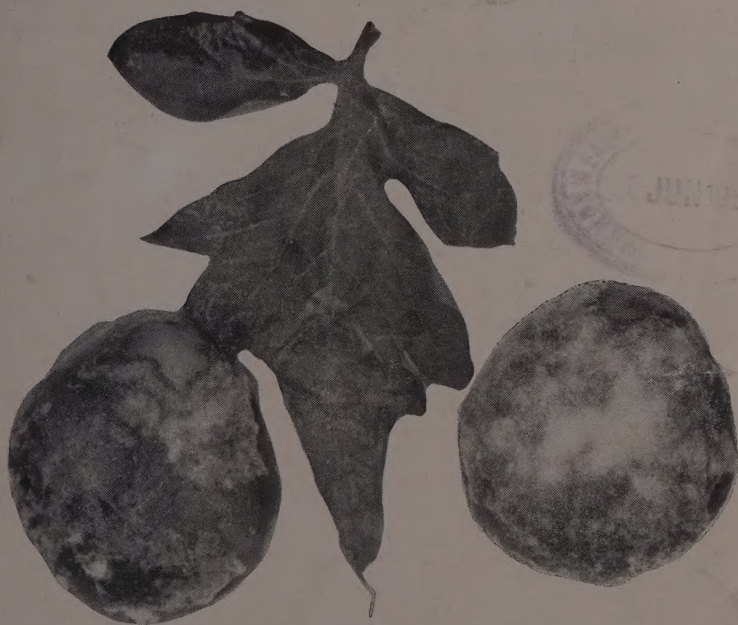
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Resistance of Certain Tomato Varieties and Crosses to Late Blight

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Late Blight in Leaf and Fruit of Marglobe Variety

Courtesy of Russell Hyre, U. S. Dept. Agr.

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RESISTANCE OF CERTAIN TOMATO VARIETIES AND CROSSES TO LATE BLIGHT

REINER BONDE AND ELIZABETH F. MURPHY¹

INTRODUCTION

The control of late blight, caused by the fungus *Phytophthora infestans* (Mont.) DeBary, is one of the most important determining factors in successful tomato production. The incidence of the disease varies greatly from season to season, at times being severe enough to cause complete crop failure and at other times being almost nonexistent. During the 1945-1946 season late blight was exceptionally severe, causing crop destruction over wide areas (9). It appeared in Florida in the fall of 1945, spread gradually as tomatoes were planted in adjacent areas, and finally infected all of the major tomato-growing areas east of the Mississippi River. From this epidemic, the total loss of the tomato crop in the United States has been estimated at \$40,000,000 (4, p. 103, 5 and 10).

The prevalence of late blight presents a real impediment to tomato production in the potato-growing part of Aroostook County, Maine. During most seasons, it is impossible to raise healthy ripe tomatoes without maintaining a schedule of frequent fungicide spraying.

The symptoms of late blight infection on tomatoes are similar to those commonly seen on potatoes.

The disease may appear on the foliage anytime during the growth of the plant. The first lesions, which are brownish or purplish black in color, are not sharply delimited but enlarge rapidly when the environment is favorable for the fungus development. A pale green zone circles the lesion. Great numbers of minute spores, which start new infection, appear as a white mildew or mold on the green zone, principally on the underside of the leaves.

Fruit may become infected at any stage of growth. The lesions first appear as gray-green water-soaked spots, which darken and enlarge infecting the entire fruit.

For several seasons, it was observed in the Aroostook Farm experimental tomato plots that some tomato varieties were relatively more resistant to late blight fruit rot than others. In 1941 and 1943, comparatively few infected fruits were observed among those of the Bounty and

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Danmark varieties whereas nearly complete fruit loss occurred among the fruits of the Bonny Best variety (1).

These observations stimulated interest in the problem of finding or developing tomato varieties which are both early maturing, for the short season characteristics of Aroostook County, and resistant to late blight. The data reported herein are those resulting from a preliminary study made to find or breed early varieties resistant to late blight.

The studies were conducted with the "common potato strain"² of the late blight fungus isolated or obtained from potato plants grown in Aroostook County, unless otherwise indicated.

From the initial observations, varieties showing resistance to late blight together with some showing desirable fruit qualities such as early maturity, large size, superior flavor or color, or high vitamin C content were chosen for further investigation. Later, new varieties were added which were found to have desirable characteristics.

GREENHOUSE TESTS FOR FOLIAGE RESISTANCE, 1949

The plants of a number of commercial varieties and the progenies of crosses between resistant and susceptible varieties were tested in a greenhouse moist chamber for foliage resistance.

Plants were grown during the spring in three-inch pots to a height of about ten inches when they were transferred to a saturated moist chamber held between 65 and 70° F. The plants were sprayed twice, with a weekly interval, using a heavy suspension of spores obtained by washing the leaves of infected Green Mountain potato plants.

Observations on infection were made two and three weeks after the second inoculation. The severity of symptoms was scored according to five degrees of defoliation (Table 1). It is obvious from these data that the foliage of Danmark, Early Dwarf, FNC 45, Red Cherry (*Lycopersicon esculentum* var. *cerasiforme*), a selection from Mexico 38211, and one from Guatemala was healthy and apparently immune or highly resistant. In addition to the above-mentioned varieties, Sun Ray seemed to show some resistance while the other 14 varieties and *L. pimpinellifolium* A and B (Table 1) were completely susceptible to foliage infection. These data confirmed those of previous field observations concerning varietal resistance to the disease. Continued work with these varieties indicates, as is discussed later in this paper, that disease resistance itself may be a relative quality, however, and that

² The strain of *P. infestans* commonly found early in the season infecting susceptible potato varieties (Green Mountain, Katahdin, etc.). It does not parasitize Kennebec.

TABLE 1

Tomato Foliage Resistance to Late Blight in Greenhouse

Variety or Cross	No. Plants Inoculated ¹	Class of Infection ²					Resistant ³	Reaction of Foliage
		1	2	3	4	5		
		%	%	%	%	%		
Abel	5				40	60	0	Susceptible
Bonny Best	2					100	0	Susceptible
Danmark	6	100					100	Resistant
Early Chatham	10				100		0	Susceptible
Early Dwarf	5	100					100	Resistant
Early Trellis	10				50	50	0	Susceptible
Fargo	2					100	0	Susceptible
FNC	2				100		0	Susceptible
FNC #45	50	98	2				100	Resistant
Guatemala ⁴	100	98	2				100	Resistant
Marglobe	20			50	50		0	Susceptible
Mexico 38211 ⁵	4	100					100	Resistant
Michigan 4502	100			25	25	50	0	Susceptible
New Hampshire 50	25				20	80	0	Susceptible
Pritchard	2				100		0	Susceptible
Quebec 5	2				100		0	Susceptible
Red Cherry	12	100					100	Very resistant
Redskin	100				50	50	0	Susceptible
Southland	5				100		0	Susceptible
Stokesdale	2				100		0	Susceptible
Sun Ray	3		100				100	Some resistance
<i>L. pimpinellifolium</i> A	12				20	80	0	Susceptible
<i>L. pimpinellifolium</i> B	6				50	50	0	Susceptible
<i>L. pimpinellifolium</i> A x Danmark F ₁	9					100	0	Susceptible
<i>L. pimpinellifolium</i> B x Danmark F ₁	6					100	0	Susceptible
Pritchard x Danmark F ₁	8		50	50			50	Some resistance
Danmark x Red Cherry F ₁	30	100					100	Resistant
Red Cherry x Danmark F ₁	8	100					100	Resistant
Red Cherry x <i>L. pimpinellifolium</i> A F ₁	6	100					100	Resistant
Danmark x Red Cherry F ₂	100	100					100	Resistant
Danmark x Red Cherry F ₃ ⁶ #1	5	100					100	Resistant
2	2	50	50 ⁷				100	Resistant
3	14	100					100	Resistant
4	5	80	20 ⁷				100	Resistant
5	1	100					100	Resistant
6	12	100					100	Resistant
7	11	100					100	Resistant
8	4	50	50 ⁷				100	Resistant
9	2	100					100	Resistant
10	7	43	57 ⁷				100	Resistant
Green Mountain Potato (Control)	2					100	0	Very susceptible
Kennebec Potato (Control)	2	100					100	Resistant

¹ All inoculations made in large damp chamber by spraying plants with spores of "common potato strain" of late blight fungus, *P. infestans*.

² Classes of infection: 1 = None noted in test.

2 = Trace small spots to 25% foliage killed.

3 = 26 to 50% foliage killed.

4 = 51 to 75% foliage killed.

5 = 76 to 100% foliage killed.

³ Includes only classes 1 and 2.

⁴ Small fruited mixed varieties. Seeds furnished by a student.

⁵ Small fruited selection from B.P.I. Accession, Mexico 38211.

⁶ Progenies from single plants selected as resistant in previous years.

⁷ Mostly "pin point" lesions.

either environment or strain of the fungus may alter the degree of resistance.

Two potato varieties were included as controls. The Green Mountain was very susceptible and was killed by the fungus. The Kennebec variety, on the other hand, developed no blight lesions during the duration of the experiment.

None of the hybrid plants of *L. pimpinellifolium* A x Danmark F_1 , *L. pimpinellifolium* B x Danmark F_1 , or Pritchard x Danmark F_1 were immune to foliage infection. The plants of Pritchard x Danmark F_1 were much more resistant than the Bonny Best controls and the other susceptible varieties included in Table 1. The resistance noted in the Danmark parent apparently imparted partial resistance to this particular cross but it was not observed in any of the other crosses. In contrast, all of the hybrids of Red Cherry by Danmark showed marked resistance but not all to the extent of the Red Cherry or the Danmark parents. Complete resistance was shown by a cross between Red Cherry and a susceptible *L. pimpinellifolium* variety. From these data it seems that Danmark possessed less inheritable resistance to foliar infection than Red Cherry.

FIELD EXPERIMENTS ON FOLIAGE AND FRUIT RESISTANCE, 1950

Plants of 11 named varieties and a number of hybrids were exposed to a severe epidemic in Aroostook County under field conditions. The infection resulted from interplanting tomatoes with susceptible Green Mountain potatoes which became naturally infected.

The foliage and fruit response of the varieties and hybrids to this natural infection from adjacent potatoes is summarized in Table 2 as recorded during the period from September 1 to September 7, just prior to a killing frost.

Ten of the 11 named varieties were shown to be completely susceptible to both foliage and fruit infection under these severe field conditions. It is noteworthy that both Danmark and Early Dwarf, which were resistant to greenhouse inoculations were extremely susceptible in the field. This reversal of response to greenhouse inoculation and natural field infection suggests that two different strains of the fungus are involved. Red Cherry, however, continued to show resistance in both foliage and fruit. This Red Cherry variety has remained healthy for five crop years at Presque Isle, Maine. It should be pointed out that plants grown from Red Cherry seed purchased in 1948 were not resistant although the plant characteristics were similar to those of the resistant strain. Other purchased seeds of this variety have not been tested but all of the studies were confined to plants originating from the selected

resistant plant. Danmark, also, was originally selected because of observed field resistance, and was later shown to be susceptible.

TABLE 2

Tomato Foliage and Fruit Resistance to Natural Late Blight Infection, 1950

Variety, Parent or Cross	No. of Plants in Test	Reaction of Foliage	Rot in Fruit Class of Infection ¹					Resistant ²
			1	2	3	4	5	
			%	%	%	%	%	%
Bonny Best	6	Very susceptible					100	0
Danmark	6	Susceptible ³					100	0
Dixville	6	Susceptible					100	0
Early Dwarf	6	Susceptible ³					100	0
James 49-39	6	Very susceptible					100	0
James 49-42	6	Very susceptible					100	0
New Hampshire 50	6	Very susceptible					100	0
Pennheart	6	Susceptible					100	0
Pritchard	3	Susceptible					100	0
Red Cherry	6	Very resistant ⁴	100					100
Trellis 22	6	Susceptible				34	66	0
Red Cherry x Danmark F ₁	12	Very resistant ⁴		92	8			92
Danmark x Red Cherry F ₁	9	Very resistant ⁴		88	12			88
Danmark x Red Cherry F ₂	45	Very resistant ⁴	16	49	21	12	2	65
(Danmark x Red Cherry) ²		Some resistance—						
x Danmark	20	variable	5	30	35	15	15	35
FNC x Sioux F ₁	3	Susceptible					100	0
Pritchard x Danmark F ₁	6	Susceptible				33	67	0
Green Mountain Potato (Control)	6	Very susceptible					100	0

¹ Classes of infection: 1 = None noted in test.

2 = 1 to 25% of the fruits rotted.

3 = 26 to 50% of the fruits rotted.

4 = 51 to 75% of the fruits rotted.

5 = 76 to 100% of the fruits rotted.

² Includes only classes 1 and 2.

³ Immune to inoculation of "common potato strain" of *P. infestans* in greenhouse.

⁴ No foliage infection in greenhouse tests.

FIGURE 1. Left. Susceptible Variety Resulting from Crossing Pritchard with Danmark. Both the foliage and fruit were very susceptible to late blight.

Right. Resistant Variety Resulting from F₂ Cross of Danmark with Red Cherry. No late blight infection occurred on foliage or fruit during a severe epidemic.



The foliage of all the F_1 and F_2 hybrids of Red Cherry x Danmark showed extreme resistance to the disease. When Red Cherry x Danmark was backcrossed to Danmark in an attempt to increase fruit size, some of the disease resistance in the foliage was lost.

The hybrids of both FNC x Sioux and Pritchard x Danmark showed extreme susceptibility in both foliage and fruit (Figure 1). No fruit rot was found in Red Cherry. Hybrids resulting from crossing Red Cherry x Danmark manifested a considerable degree of resistance to fruit rot, especially early in the season. Some developed in these hybrids as the season advanced, however. Ninety-two and 88 per cent respectively of the F_1 plants were recorded as Class 2 (1 to 25 per cent of the fruits rotted) and may be considered resistant. It is also noteworthy that 16 per cent of the F_2 progeny of Danmark x Red Cherry were free of fruit rot. Figure 1 depicts a plant of this cross which was free of infection in the foliage and the fruit.

FIELD EXPERIMENT, 1951

A field experiment was repeated in 1951 to obtain additional information on the resistance of named varieties and on the Red Cherry crosses.

The plants, started in the greenhouse, were field-set in a location favorable for infection. Unsprayed susceptible Green Mountain potatoes were interplanted with the tomatoes to serve as a source of inoculum. To be certain of infection, the potato plants were inoculated with spores of the pathogen.

The 1951 conditions were favorable for spread of the disease throughout the entire season. Potato infection in Aroostook County caused more than usual loss³ and the crop of unsprayed garden tomatoes was a total failure.

Foliage Infection in Different Varieties and Progenies. The percentage of defoliation by the disease for the different varieties and progenies included in the test was recorded on August 28 and September 13. The results are noted in Table 3 (columns 2 and 3). All of the named varieties under test proved to be susceptible to foliage infection. There were apparent, however, differences among varieties in the degree of infection that occurred. For example, on September 13, Danmark and Pennheart manifested considerable foliage resistance whereas Bonny Best, Fargo, and New Hampshire 50 showed extreme susceptibility. Fargo was consistently the first to become infected in the field tests.

³ Many potato growers considered the 1951 crop year as one of the worst for late blight in the history of Maine.

TABLE 3

Tomato Foliage and Fruit Resistance to Natural Late Blight Infection, 1951

Variety or Cross ¹	Foliage ²		Fruit, August 28	
	August 28	September 13	No. Observed	Rotted
	%	%		%
Abel	9.0	23.5	17	70.6
Bonny Best	40.5	55.6	24	50.0
Danmark	12.0	15.0	53	5.7
Fargo	40.5	88.0	44	100.0
FNC	4.0	40.5	25	8.0
New Hampshire 50	23.5	94.0	27	8.7
Pennheart	8.0	14.0	15	33.3
Scarlet Dawn	40.5	40.5	8	0.0
Stokescross #1	23.5	25.0	27	55.6
Danmark x Red Cherry F ₃ ³	0.0	1.2	120	0.0
" " "	4.0	8.5	94	6.4
" " "	0.0	0.2	164	1.2
" " "	0.0	0.8	114	0.0
" " "	0.0	8.0	116	0.9
" " "	0.0	5.0	125	0.0
" " "	0.0	23.5	125	0.0
" " "	0.0	40.5	125	0.0
" " "	0.0	26.5	118	17.0
" " "	0.0	10.5	77	0.0
" " "	0.0	33.0	117	3.4
(Danmark x Red Cherry) F ₂ x Danmark	23.5	33.0	101	52.0
" " "	23.5	59.5	71	30.8
" " "	13.5	15.0	91	21.0
(Danmark x Red Cherry x Danmark) x Trellis 22	16.0	59.5	99	28.3
" " "	3.5	12.0	101	5.0
" " "	9.0	10.5	45	62.2
Red Cherry x Early Dwarf	0.0	6.0	51	5.9
" " "	0.8	5.0	99	3.0

¹ Data from five plants for each variety or cross.² Determination of foliage infection adopted from R. W. Barrett and J. G. Horsfall. "An Improved Grading System for Measuring Plant Diseases" Mimeographed sheets.³ Progeny from resistant plants selected in 1950.

The foliage reaction of all of the selections from Danmark x Red Cherry F₃ showed high resistance. Ten of the 11 tested were free of infection on August 28, and seven were still relatively free of the disease (trace to 10.5 per cent) on September 13.

Of many named tomato varieties tested for adaptability to the Maine climate and surveyed for resistance,⁴ the few which manifested resistance were small-fruited. Danmark, which averages approximately 2.5 ounces per fruit under Maine conditions (8) was the largest-fruited variety to show any degree of resistance. The progeny of resistant selections from Danmark x Red Cherry F₃ were small fruited. For this reason it was decided to backcross the resistant Danmark x Red Cherry hybrids not only to Danmark but to a susceptible larger-fruited variety which is early maturing and superior in vitamin C. Trellis 22 was chosen because it had these qualities. The F₁ progeny of both the Danmark and Trellis 22 backcrosses lost part of the resistance of the Danmark x Red Cherry hybrids.

⁴ For purposes of brevity, many varieties observed to be susceptible are not reported in this paper.

Fruit Infection in Different Varieties and Progenies. The amount of fruit rot present in the different varieties and hybrids tested during 1951 is shown in Table 3, column 5, as percentage of number of fruits infected. All of the named varieties with the exception of Danmark, FNC, Scarlet Dawn, and New Hampshire 50, showed a high percentage of fruit rot. Fargo, a yellow pear type (*L. esculentum* var. *pyriforme*) had all of the fruit infected. Scarlet Dawn (with only eight fruits matured) showed no fruit decay on August 28. Danmark and New Hampshire 50 showed respectively only 8.0 to 3.7 per cent of the fruit rotted.

All of the Danmark x Red Cherry F_1 selections possessed a high degree of resistance to fruit rot when examined on August 28. Fruits from six of the 11 selections developed no rot and those from four other selections showed only 0.9 to 6.4 per cent.

The F_1 fruits resulting from backcrossing Danmark x Red Cherry with Danmark appeared to have lost most of their resistance and the percentage of fruit loss was much greater than in Danmark.

The cross Red Cherry x Early Dwarf F_1 showed relatively little fruit rot on August 28 indicating some resistance. The same is true of one of the crosses with Trellis 22 as one parent.

PERMANENCE OF RESISTANCE

A significant phenomenon brought out in this investigation was the variability of resistance in certain tomato varieties during different crop years. Danmark, for example, showed little or no infection in a number of early yield tests in contrast to the complete susceptibility of Bonny Best. As a result, Danmark was chosen as parent material in an attempt to introduce resistance into other varieties. Similarly, Scarlet Dawn³ in 1950 was relatively free of fruit rot compared with the high percentage in a number of commercial varieties grown under the same conditions. Continued observations showed that these two varieties were less resistant than was previously believed, however. Further study may clarify the discrepancy.

There is not always a consistent relationship between foliage resistance and fruit resistance. That is, foliage may be relatively healthy but fruit from the same plant susceptible, confirming the results of other investigators [2 and 6]. On the other hand, observations indicate that generally plants having fruit resistance also are likely to show some degree of foliage resistance. However, foliage resistance should be used with caution as a prognostic of fruit resistance.

³A variety supplied by Professor F. H. Steinmeier and believed to be called Scarlet Dawn.

It appeared that a variety or hybrid may manifest resistance to infection early in the season in relation to other varieties but become more susceptible as the season advances. This was demonstrated when the foliage of Red Cherry and the F_3 progeny of Danmark x Red Cherry were immune to infection by the "common potato strain" of the fungus in greenhouse experiments (Table 1). Later, similar progenies of Danmark x Red Cherry were immune or highly resistant to field infection early in the season (August 28), but showed greater susceptibility at a later date (September 13) when the degree of defoliation of the plants varied from a trace to 40.5 per cent (Table 3).

The same phenomenon commonly occurs with certain resistant Maine potato varieties. Sebago possesses a considerable degree of resistance and sometimes escapes serious defoliations under field conditions which kill plants of Green Mountain, Irish Cobbler, and the other susceptible varieties. Sebago, however, has been known to be completely destroyed by blight later in the season. Again, the Kennebec potato variety is known to be immune to the "common potato strain" of the late blight fungus. Under prolonged conditions favorable to blight infection, however, the Kennebec variety was observed to develop a few late blight lesions.⁶ During the serious 1951 epidemic, the writers observed a field of Kennebec potatoes which was severely infected with late blight.

The writers' observations for a number of years suggest that virulent strains of the fungus may arise on resistant varieties and from there be disseminated. The degree to which the virulent strain attacks the crop depends on the length of growing season and the prevailing weather conditions. Recently de Bruyn (3) confirmed this observation, showing that the *P. infestans* fungus has great plasticity. She reported that virulence increases by passages through resistant plants, when they become occasionally susceptible by altered environmental conditions.

The Red Cherry appeared to be homozygous as regards the resistance factor, and the behavior of the progeny suggests that the resistance is dominant. Danmark, on the other hand, may be inherently only partly resistant to the disease, or, more likely, may be resistant to certain types of inoculum but susceptible to other, more virulent, strains. Further study is needed to clarify these points.

As far as can be determined, the fungus involved in these investigations was the potato strain of *P. infestans*. Mills (7) has shown that the tomato strain originates as a result of serial passage of the potato strain through tomato foliage. In the greenhouse tests here reported (Table 1), the inoculum could not possibly have built up virulence by passage

⁶ Schultz, E. S. and Bonde, R. Unpublished data.

through tomato foliage and yet severe defoliation resulted in some varieties and hybrids. However, in later field epidemics, opportunity was provided for increase in virulence by passage through tomato foliage. In 1949 and 1950, all cultures from field infected fruit were identified as potato strain.⁷

SUMMARY

Twenty-one commercial tomato varieties (*L. esculentum*), two varieties of *L. pimpinellifolium*, and the progeny of five crosses were observed for foliage resistance to the "common potato strain" of late blight in the greenhouse. Of the varieties, six showed foliage resistance. F_1 progenies of Danmark (resistant) \times susceptible varieties manifested partial to total susceptibility. F_1 progenies of Red Cherry (resistant) with *L. pimpinellifolium* (susceptible) and with Danmark showed high resistance. F_3 progenies of Danmark \times Red Cherry manifested a high degree of resistance.

Plants of 11 varieties and the progenies of several crosses were subjected to natural field infection by late blight in 1950. Only Red Cherry of the varieties showed both foliage and fruit resistance. All of the other varieties were susceptible, including two which had previously been foliar resistant to greenhouse inoculum. The Danmark \times Red Cherry progenies were resistant. Backcrossing to Danmark lowered the foliage resistance.

Nine varieties and the progenies of four crosses involving a Red Cherry parent were subjected to a severe field epidemic of late blight in 1951. Four varieties showed some fruit resistance (0 to 8.0% decay) but not always corresponding foliage resistance (16 to 94% defoliation). Danmark \times Red Cherry F_3 progeny showed practically no fruit decay in 55 plants, all of the plants manifested foliage resistance in August and more than half of the plants were less than 10 per cent defoliated in September. Backcrossing to Danmark and Trellis 22 increased both fruit decay and foliage lesions.

Red Cherry was the only variety which consistently manifested high foliage and fruit resistance to both natural and induced late blight infection. The behavior of its progeny indicated that its resistance is a dominant characteristic. Evidence is presented which indicates that there are strains of *P. infestans* which vary in their ability to attack the different tomato varieties.

⁷ The strains were identified by Russell Hyre, Pathologist, Division of Mycology and Disease Survey, United States Department of Agriculture, University of Delaware, Newark, Delaware.

The data indicate that commercial varieties of tomatoes can be developed that will be highly resistant or immune to foliage and fruit infection by *P. infestans*.

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